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Abstract. In order to understand the response of gross primary production (GPP) and above-ground biomass (AGB) to warming, a field warming experiment using open-top chambers was conducted in an alpine meadow at three elevations (i.e., 4313, 4513, and 4693 m) on the Northern Tibetan Plateau in May 2010. We calculated GPP from the moderate-resolution imaging spectroradiometer algorithm and AGB using the surface measured data in 2012. Average GPP and AGB at elevation 4313 m was significantly decreased by experimental warming, whereas the declines at elevations 4513 and 4693 m were not statistically significant across all sampling dates. The negative effects of experimental warming on GPP and AGB may be related to experimental warming-induced soil drying. The different responses of GPP and AGB to experimental warming among the three alpine meadow sites could be dependent on climate conditions. Our findings suggested that experimental warming did not enhance GPP and AGB in the alpine meadow, and its effects differed among alpine meadows on the Tibetan Plateau. © *The Authors. Published by SPIE under a Creative Commons Attribution 3.0 Unported License. Distribution or reproduction of this work in whole or in part requires full attribution of the original publication, including its DOI.* [DOI: 10.1117/1.JRS.7.073505]

1 Introduction

Gross primary production (GPP) and above-ground biomass (AGB) play important roles in the carbon cycling of terrestrial ecosystems and are related to plant growth, ecosystem respiration, and net ecosystem exchange.[1–4] Understanding the response of GPP and AGB to warming is crucial for predicting future changes in the carbon cycling. Inconsistent results on the response of GPP and AGB to warming have been observed with respect to vegetation types and climate conditions.[5–8]

Experimental warming is a key tool for understanding the effects of climate change on various terrestrial ecosystems, and various warming simulation equipment has been applied worldwide.[9–11] As one of the most prevalent warming simulation approach, open-top chambers (OTCs) have their own attributive advantages, such as being cheap and transportable and requiring no electricity and high-level technique equipment,[12,13] and thereby are very suitable for remote areas where electricity is often a limiting factor. In addition, OTCs probably alter relative humidity, precipitation, and wind speed, whereas the unwanted effects are not always significant.[9,12,13] However, OTCs have been widely applied in various ecosystems, including arctic

tundra ecosystems,[14,15] alpine meadows,[16,17] swamp meadows,[18] salt marshes,[19] forest ecosystems,[20] and agriculture ecosystems.[21]

The Tibetan Plateau is experiencing significant climate warming, and the expected warming trend is much greater than average.[22,23] The alpine meadow plays a key role in the region carbon budget in China[3,24] and is one of the most sensitive terrestrial ecosystems to climate change among various grasslands in China.[25,26] About one-third of the Tibetan Plateau is covered with alpine meadow, which is one of the major pasturelands on the Tibetan Plateau.[27,28] Many warming experiments have been performed in the alpine meadow on the Tibetan Plateau in order to understand their responses to warming, whereas there are still uncertainties about warming effects on carbon flux.[16–18,29] On the other hand, only a few studies are focused on the response of GPP and AGB to warming in the alpine meadow of Tibet along an elevation gradient. Therefore, here we set up a field warming experiment in an alpine meadow at three elevations (i.e., 4313, 4513, and 4693 m) on the Northern Tibetan Plateau to investigate warming effects on GPP and AGB.

A recent meta-analysis showed that experimental warming enhanced ecosystem photosynthesis and AGB.[30] Therefore, we hypothesized that experimental warming could increase GPP and AGB of alpine meadow in this study.

2 Materials and Methods

2.1 *Study Area*

The study area (30°30′ to 30°32′ N, 91°03′ to 91°04′ E) was located at Damxung Grassland Observation Station, Tibet Autonomous Region of China. The annual mean sunlight is 2880.9 h and the annual mean solar radiation is 7527.6 MJ m^{-2}. The annual mean air temperature is 1.3°C, ranging from the lowest value (−10.4°C) in January to the maximum (10.7°C) in July. Annual mean precipitation is around 476.8 mm, with >80% occurring in the period from June to August.[3] The annual potential evapotranspiration is ~1725.7 mm. The soil freezing duration is from November to January. The soil texture is sandy loam. The soil layer is 0.5 to 0.7 m thick, with organic matter of 0.3 to 11.2%, total nitrogen of 0.03 to 0.49%, and pH of 6.0 to 6.7.[28] The typical vegetation type in the study area is *Kobresia*-dominated alpine meadow.[26] Roots are mainly concentrated in the topsoil layer (0 to 20 cm). Annual air temperature significantly increased 1.6°C, while change in annual precipitation was not significant from 1963 to 2010 in this study area.[8]

2.2 *Experimental Design*

The experiment was set up on a south-facing slope on the Nyainqentanglha Mountains at three elevations (i.e., 4313, 4513, and 4693 m). Four OTCs were randomly established at each alpine meadow site in May 2010. The OTCs were 1.45 and 1.00 m in bottom and top diameters and 0.40 m in height.[26] The OTCs were made of 3-mm thick polycarbonate. The OTCs remained on the plots year round. One control plot was randomly set up in the vicinity of each OTC. There was ~3 m distance between plots.

Soil temperature at the depth of 0.05 m, soil water content at the depth of 0.10 m (SWC), air temperature (T_a), and relative humidity (RH) at the height of 0.15 m were continuously auto-monitored using meteorological towers. All the channels were connected to data loggers (HOBO weather station, Onset Computer, Bourne, MA). Vapor pressure deficit (VPD) was the difference between saturation and actual vapor pressures, which were calculated using measured T_a and RH.[3] Experimental warming significantly increased daily T_a by 1.08, 1.81, and 0.94°C and daily VPD by 0.05, 0.05, and 0.03 kPa at elevations 4313, 4513, and 4693 m from June to September in 2012, respectively. In contrast, daily SWC was significantly decreased by −0.05, −0.03, and −0.03 m^3 m^{-3}, respectively, at elevations 4313, 4513, and 4693 m. OTCs-induced increment in T_a and VPD and decrement in SWC were in line with previous studies that indicated the warming and drying trends across the Tibetan Plateau.[31,32] Daily T_a and VPD during the study period significantly decreased with increasing elevation along the elevation gradient (4313 to 4693 m),

whereas daily SWC significantly increased with increasing elevation. Precipitation increases with increasing altitude along the elevation gradient.[8] However, there were no significant differences between control and warmed plots for canopy coverage and topsoil (0 to 20 cm) microbial biomass in August 2011.[26]

2.3 *Normalized Difference Vegetation Index*

Photographs in a 0.5 m × 0.5 m subplot in the center of each plot were taken using a Tetracam Agricultural Digital Camera (ADC, Tetracam Inc., Chatsworth, CA) for each plot from late June to September in 2012. The camera has green (520 to 600 nm), red (630 to 690 nm), and near-infrared (760 to 900 nm) bands. The camera can produce 2048 pixels × 1536 pixels with an 8.0-mm lens. When any one study target photograph was taken, the lens of ADC was parallel to the ground and the height of the ADC was ~1.0 m to limit the variations in spatial resolution and field of view. At the height of 1.0 m, the spatial resolution and field of view are ~0.4 mm and 0.8 m × 0.6 m, respectively. The field of view (0.8 m × 0.6 m) is larger than that of the ground target view (0.5 m × 0.5 m) to reduce the edge effect. Calibration photographs of a white Teflon plate provided by the Tetracam manufacturer were taken before and after each batch of the study target photographs. The calibration photographs were also taken when light condition changed remarkably. All the study target photographs were processed using the PixelWrench2 software (included with the ADC) to obtain normalized difference vegetation index (NDVI), and photographs of the white Teflon calibration plate were used to produce the calibration parameters.[33,34] Band saturation may occur, which could reduce the dynamic range of NDVI.[35] Since the NDVI value was <0.7 in our study area, the NDVI saturation could not generally happen.

In addition, we used the moderate-resolution imaging spectroradiometer (MODIS) vegetation indices data (MOD13A3, Collection 5, 1 km spatial resolution and monthly composite temporal resolution) over the Tibetan alpine meadow from June to September during 2000 to 2012.

2.4 *GPP Algorithm*

GPP was calculated based on the MODIS GPP algorithm. Our previous one study has validated the GPP algorithm using surface observed data in an alpine meadow of Tibet, which is near to our study sites.[3] The MODIS GPP algorithm is based on a light use efficiency (LUE) approach.[36] LUE is combined with absorbed photosynthesis active radiation (PAR) by vegetation canopy (APAR) to calculate GPP ($g\,C\,day^{-1}$) as follows:

$$GPP = LUE \times APAR. \tag{1}$$

LUE is calculated as

$$LUE = LUE_{max} \times T_{a\,min\_scalar} \times VPD\_scalar, \tag{2}$$

where LUE_{max} is the maximum light use efficiency or the ecosystem apparent quantum yield ($g\,C\,MJ^{-1}$). The LUE_{max} was set to be 0.81 $g\,C\,MJ^{-1}$ in this study.[3] $T_{a\,min\_scalar}$ and VPD_scalar are the two attenuation scalars with a range from 0 to 1. Daily minimum T_a ($T_{a\,min}$) and daytime average VPD were used to calculate $T_{a\,min\_scalar}$ and VPD_scalar as follows:[36]

$$T_{a\,min\_scalar} = \begin{cases} 0, & T_{a\,min} < T_{a\,min\_min} \\ \frac{T_{a\,min} - T_{a\,min\_min}}{T_{a\,min\_max} - T_{a\,min\_min}}, & T_{a\,min\_min} < T_{a\,min} < T_{a\,min\_max}, \\ 1, & T_{a\,min} > T_{a\,min\_max} \end{cases} \tag{3}$$

$$VPD\_scalar = \begin{cases} 0, & VPD > VPD_{max} \\ \frac{VPD_{max} - VPD}{VPD_{max} - VPD_{min}}, & VPD_{min} < VPD < VPD_{max}. \\ 1, & VPD < VPD_{min} \end{cases} \tag{4}$$

APAR can be calculated as

$$APAR = PAR \times FPAR, \tag{5}$$

where FPAR is the fraction of absorbed PAR by the vegetation canopy. FPAR was estimated using the observed NDVI values in this study as follows:[37]

$$FPAR = \frac{FPAR_{NDVI} + FPAR_{SR}}{2}, \tag{6}$$

$$FPAR_{NDVI} = \frac{(NDVI - NDVI_{min})(FPAR_{max} - FPAR_{min})}{NDVI_{max} - NDVI_{min}} + FPAR_{min}, \tag{7}$$

$$FPAR_{SR} = \frac{(SR - SR_{min})(FPAR_{max} - FPAR_{min})}{SR_{max} - SR_{min}} + FPAR_{min}, \tag{8}$$

$$SR = \frac{1 + NDVI}{1 - NDVI}, \tag{9}$$

where $FPAR_{max} = 0.95$ and $FPAR_{min} = 0.001$, respectively.[37]

In this study, we used different model parameters to calculate GPP (Table 1).[3,37]

2.5 AGB Estimation

AGB was estimated using a nondestructive approach.[38] Briefly, photographs were also taken using the ADC outside the treatment plots and then above-ground plant parts were harvested, dried, and weighed in the three alpine meadow sites along the elevation gradient during the growing season in 2012. A regression equation ($AGB = 10.33e^{3.28NDVI}$, $R^2 = 0.64$, $p < 0.001$, $n = 135$) between AGB and NDVI was developed using the data collected from outside the treatment plots across the three alpine meadows along the elevation gradient.

2.6 Statistical Analysis

For a specific site, repeated-measures analysis of variance was used to estimate the main and interactive effects of experimental warming and sampling dates on GPP and AGB. Linear regression analyses between GPP, AGB and T_a, SWC were conducted, respectively. All the statistical analyses were performed using the SPSS software (version 16.0; SPSS Inc., Chicago, IL).

3 Results and Discussion

Based on averaging the air temperature and precipitation data of all the 38 weather stations in Tibet, the mean air temperature (June to September) showed a significant increase trend ($0.08°C\,yr^{-1}$), while average total precipitation showed an insignificant decrease trend ($-5.5\,mm\,yr^{-1}$) from 2000 to 2012 (Fig. 1). On the other hand, there was no significant positive trend (slope $= 0.0004$) for MODIS-based NDVI over the Tibetan alpine meadows during the past 13 years (2000 to 2012) (Fig. 1). However, ~4.7 and 2.9% of the alpine meadow area showed significant increase and decrease trends, respectively (Fig. 2). Therefore, warming could not always increase NDVI.[31] This finding was supported by the effects of experimental warming on NDVI in the alpine meadow at the three elevations. In detail, experimental warming significantly decreased the average NDVI by 15.6% at elevation 4313 m ($F = 11.81$, $p < 0.05$), but only tended to decrease the average NDVI by 8.1% ($F = 0.88$, $p = 0.39$) and 5.6% ($F = 1.26$, $p = 0.30$) at elevations 4513 and 4693 m, respectively.

Table 1 Values for $T_{a\,min\_max}$ (°C), $T_{a\,min\_min}$ (°C), VPD$_{max}$ (kPa), VPD$_{min}$ (kPa), NDVI$_{min}$, NDVI$_{max}$, SR$_{max}$, and SR$_{min}$ used in gross primary production (GPP) calculation and average GPP (g C m^{-2} d^{-1}) comparisons between the control plots and open-top chambers (OTCs) across all the measuring dates at elevations 4313, 4513, and 4693 m, respectively.

| Model	$T_{a\,min\_max}$	$T_{a\,min\_min}$	VPD$_{max}$	VPD$_{min}$	NDVI$_{max}$	NDVI$_{min}$	SR$_{max}$	SR$_{min}$	4313 m		4513 m		4693 m	
									Control	OTC	Control	OTC	Control	OTC
GPP1	12.02	−8.00	3.50	0.65	0.760	0.015	7.333	1.030	1.17	0.91[a]	1.73	1.58	1.69	1.58
GPP2	12.02	−8.00	4.10	0.65	0.760	0.015	7.333	1.030	1.18	0.92[a]	1.70	1.53	1.70	1.56
GPP3	11.39	−8.00	3.10	0.65	0.760	0.015	7.333	1.030	1.21	0.93[a]	1.74	1.55	1.75	1.60
GPP4	11.39	−8.00	3.50	0.65	0.760	0.015	7.333	1.030	1.22	0.94[a]	1.75	1.56	1.75	1.60
GPP5	11.39	−8.00	4.10	0.65	0.760	0.015	7.333	1.030	1.22	0.95[a]	1.75	1.58	1.75	1.61
GPP6	12.02	−8.00	3.10	0.65	0.760	0.015	7.333	1.030	1.17	0.90[a]	1.69	1.51	1.69	1.55
GPP7	12.02	−8.00	3.50	0.65	0.795	0.015	8.756	1.030	1.08	0.84[a]	1.58	1.44	1.54	1.44
GPP8	12.02	−8.00	4.10	0.65	0.795	0.015	8.756	1.030	1.08	0.85[a]	1.55	1.40	1.54	1.41
GPP9	11.39	−8.00	3.10	0.65	0.795	0.015	8.756	1.030	1.11	0.86[a]	1.59	1.42	1.59	1.45
GPP10	11.39	−8.00	3.50	0.65	0.795	0.015	8.756	1.030	1.11	0.87[a]	1.59	1.43	1.59	1.46
GPP11	11.39	−8.00	4.10	0.65	0.795	0.015	8.756	1.030	1.11	0.87[a]	1.60	1.44	1.59	1.46
GPP12	12.02	−8.00	3.10	0.65	0.795	0.015	8.756	1.030	1.07	0.83[a]	1.54	1.38	1.54	1.40

[a] $p < 0.01$.
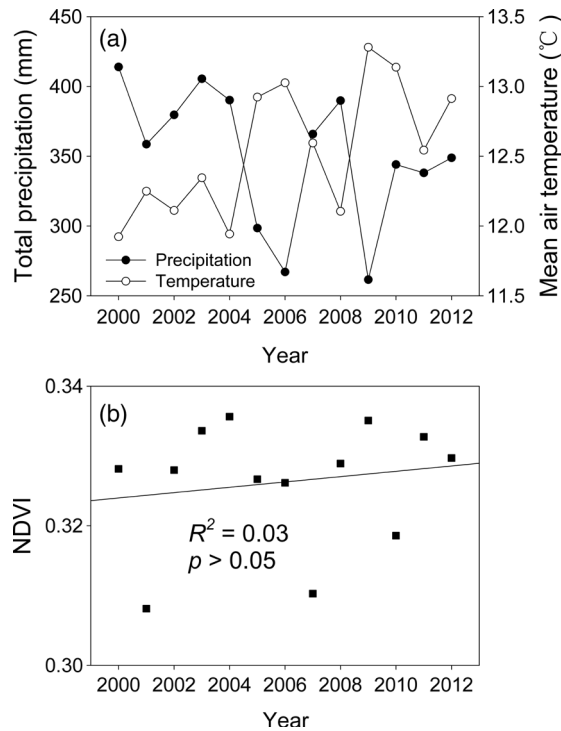
Fig. 1 The variations of (a) mean air temperature (°C) and total precipitation (mm) and (b) spatial average normalized difference vegetation index (NDVI) over Tibetan alpine meadow during 2000 to 2012. The data during the period from June to September were used.

GPP and AGB showed similar seasonal dynamics among the three alpine meadow sites regardless of experimental warming, respectively (Fig. 3). The significant seasonal changes of GPP and AGB were similar to previous studies.[39–41]

The average GPP in the control and warmed plots at elevations 4313, 4513, and 4693 m were 1.07 to 1.22 $g\,C\,m^{-2}\,d^{-1}$ and 0.83 to 0.95 $g\,C\,m^{-2}\,d^{-1}$, 1.54 to 1.75 $g\,C\,m^{-2}\,d^{-1}$ and 1.38 to 1.58 $g\,C\,m^{-2}\,d^{-1}$, and 1.54 to 1.75 $g\,C\,m^{-2}\,d^{-1}$ and 1.40 to 1.61 $g\,C\,m^{-2}\,d^{-1}$,
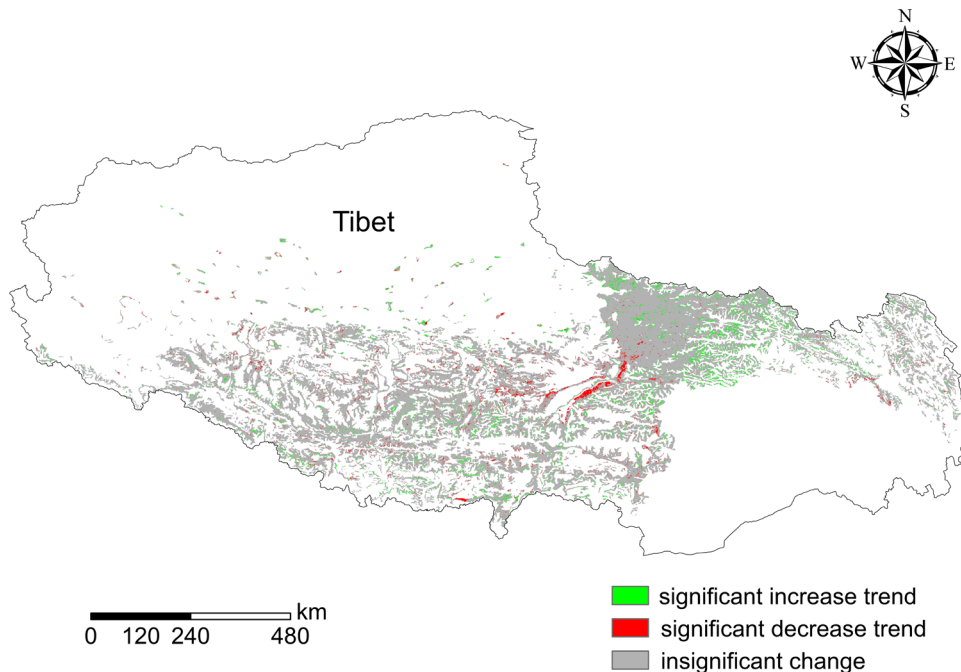

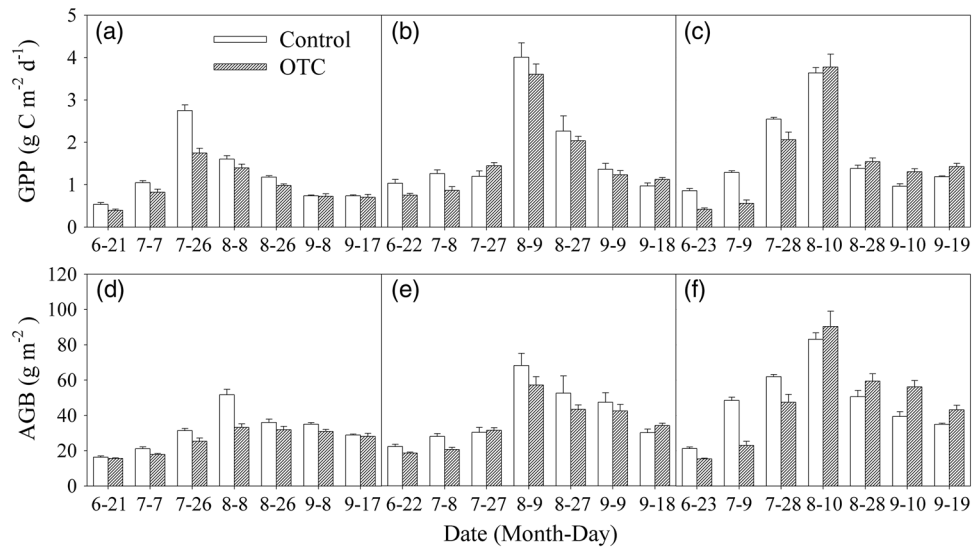**Fig. 2** Change trend of NDVI in Tibetan alpine meadow during 2000 to 2012.

Fig. 3 Effects of experimental warming on gross primary production (GPP, $g\,C\,m^{-2}\,d^{-1}$) and above-ground biomass (AGB, $g\,m^{-2}$) in the three alpine meadow sites located at elevations 4313 m [(a) and (d)], 4513 m [(b) and (e)], and 4693 m [(c) and (f)] on the Northern Tibetan Plateau, respectively. Error bars represent standard errors ($n = 4$). Here GPP data were GPP1.
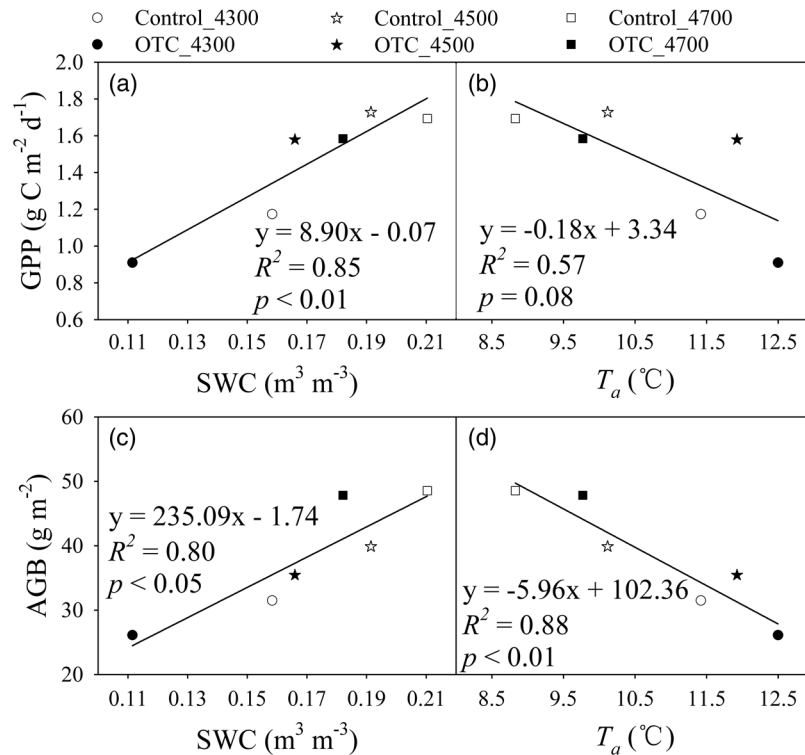

Fig. 4 Relationships among growing-season average GPP ($g\,C\,m^{-2}\,d^{-1}$), AGB ($g\,m^{-2}$), and soil water content ($m^3\,m^{-3}$) [(a) and (c)] and between growing-season average GPP, AGB, and air temperature (T_a, °C) [(b) and (d)] across elevation and warming treatment in the alpine meadow on the Tibetan Plateau. Here GPP data were GPP1.

respectively, which were close to previous observations conducted near our study sites.[3,40]

The average AGB in the control and warmed plots at elevations 4313, 4513, and 4693 m were 31.49 g m^{-2} and 26.12 g m^{-2}, 39.86 g m^{-2} and 35.43 g m^{-2}, and 48.54 g m^{-2} and 47.84 g m^{-2}, respectively, which were close to previous observations conducted near our study sites.[41,42] However, AGBs in this study were much lower than the reported values in the alpine meadow of Haibei Alpine Meadow Ecosystem Research Station.[43] The difference between the two studies was probably due to SWC in the Haibei Alpine Meadow Ecosystem Research Station being larger and the growing-season average T_a in the Haibei Alpine Meadow Ecosystem Research Station being closer to the optimum T_a in the alpine meadow on the Tibetan Plateau compared to this study.[8,26]

Contrary to our expectation, experimental warming significantly decreased average GPP and AGB by 21.7 to 23.0% and 17.1% at elevation 4313 m across all the sampling dates, respectively ($p < 0.05$). However, the declines of average GPP and AGB at elevations 4513 and 4693 m were not statistically significant. The negative effects of experimental warming on average GPP and AGB were in accordance with some previous studies.[6,7,44,45]

GPP and AGB significantly increased with increasing SWC across warming treatments along the elevation gradient (Fig. 4). The positive relationships among GPP, AGB, and SWC were in line with previous studies.[5,8,39,40,46] Similarly, Reichstein et al.[36] showed that a limitation of water caused a reduction in GPP during the European 2003 summer. Fu et al.[3] found that GPP during the 2006 summer was largely decreased by soil drying in an alpine meadow of Tibet compared to other years. Fu et al.[39] indicated that GPP was positively correlated with SWC across three grass-lands in China. AGB of alpine grassland increased with precipitation at various spatial scales on the Tibetan Plateau.[4,8] Li et al.[18] indicated that AGB of a swamp meadow was significantly larger than that of an alpine meadow due to a higher SWC in the Fenghuoshan region on the Tibetan Plateau. Therefore, experimental warming-induced significant or fractional declines in GPP and AGB may be partly related to experimental warming-induced soil drying.[6,18,47,48]

GPP was weakly decreased with increasing T_a, while AGB was significantly reduced across warming treatments along the elevation gradient (Fig. 4). This finding was in accordance with some previous studies, which indicated that there was optimum temperature for GPP and AGB at various spatial scales.[5,8,48,49] Therefore, experimental warming-induced increment in T_a was probably beyond the optimum temperature for GPP and AGB. However, the relationships among GPP, AGB, and T_a were regulated by water availability.[3,8,18]

The different responses of GPP and AGB to experimental warming among the three alpine meadow sites could be dependent on different soil moisture and T_a conditions.[8,18] The optimum T_a was ~5.8°C for AGB in the alpine meadow of Tibet.[8] GPP and AGB increased with increasing water availability.[3,4] In this study, T_a at elevation 4693 m was closest to the optimum T_a and water availability increased with increasing elevation. That is, experimental warming-induced warmer and drier conditions deviated from the optimum T_a and water availability conditions for GPP and AGB, while the deviation magnitude may decrease with increasing elevation. Similarly, the largest declines in GPP caused by experimental warming occurred in summer when warming-induced drying stress was the highest.[6] The lesser decrease of GPP caused by summer drought in an evergreen forest compared to a deciduous forest may be attributed to its relative high SWC condition during normal years.[50]

4 Conclusions

In summary, experimental warming did not increase GPP and AGB in the alpine meadow of Tibet. The responses of GPP and AGB to experimental warming varied with alpine meadows and were regulated by water availability on the Tibetan Plateau.

Acknowledgments

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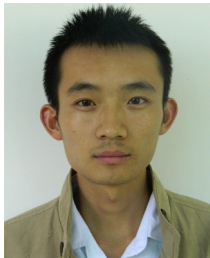
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